Oviposition on Peripheral Hosts by Dispersing *Pieris napi* (L.) (Pieridae)

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Abstract. Females of *Pieris napi* dispersing through an unfavourable habitat were able to detect *Cardamine flexuosa L.* individuals hidden from sight. Such peripheral hostplants receive more *P. napi* eggs than conspecifics at the population centre; this is partly due to females laying several eggs at a single visit, apparently a tactic adopted in response to low hostplant density. Inverse density-dependent host selection may have important effects on hostplant communities, such as increased herbivore pressure on peripheral host species.

Introduction

Several recent investigations have reported that individuals within a butterfly population may adopt different reproductive tactics in response to environmental variation (Wiklund, 1981; Tabashnik et al., 1981). For instance, females experiencing low availability of foodplants may respond by ovipositing more readily upon suboptimal hosts (Singer, 1982, 1984) or by increasing the number of eggs deposited on a host (Parker and Courtney, 1984). Further observations are badly needed to document the factors which influence such changes in behaviour. However, it is normally hard to make extensive observations on females in marginal habitats, where the insects are, by definition, scarce. I report here observations on *Pieris napi* (L.) at Delamere Forest, Cheshire, England, where individual females were regularly watched during July and August 1982, as they entered apparently unfavourable habitats during dispersal from population centers. Several unusual behaviours were seen, and are described here because of their importance to population and community processes.

Observations and Results

Two population centres for *C. flexuosa* were found in wet meadows to the north-east of Delamere. *Nasturtium officinale* R. B and *Cardamine pratensis* L. (both Cruciferae) were the predominant hostplants, with some *C. flexuosa*. Both populations bordered a large coniferous plantation which contained felled areas where Bracken (*Pteridium aquilinum* L.) and Bramble (*Rubus fructicosus* L. agg.) grew densely. 600 m of trees separated the two marshy areas where, in July-August, the second brood of *P. napi* was in good numbers, making short flights among the

Table 1. Individuals of *P. napi* observed in two areas of Delamere Forest on 28.7. and 4.8.1982. Comparison of the main population (marsh) with dispersing individuals (heath) yields a significant difference in sex-ratio ($X^2 = 5.906$ $p < 0.025$).

P. napi		*Marsh*	*Heath*
	Males	32	17
	Females	8	15

vegetation. A few butterflies were also seen in the felled areas of the plantation, flying rapidly and directly across the apparently unsuitable habitat. The sex ratios of individuals in the marsh and heathland areas were significantly different: proportionately more females were seen away from the main population areas (Table 1). This difference probably arises more from differential conspicuousness of the two sexes in the main population areas (Gilbert and Singer, 1975) than from differential dispersal of the sexes (e.g., Shapiro, 1970). No differences were found in spermatophore counts of five females from either habitat; all females had mated once.

On 28th July, two females were observed in the felled area in characteristic "oviposition search" style of flight, which is adopted in the vicinity of hostplants (Chew, 1975; Wiklund and Ahrberg, 1978). Close inspection showed that these females had located a small group of *C. flexuosa* plants, growing in an old, moist ditch underneath the Bracken. These hostplants were located 900 m away from each of the two marshy areas. The hostplants were largely hidden from sight below the Bracken, and subsequent observation on other *P. napi* individuals confirmed that females did not visually detect the *C. flexuosa* patch. Butterflies were, on several occasions, seen to switch, from rapid, direct flight to slow, host-location flight, when in the vicinity of completely hidden *C. flexuosa*. Olfactory stimulation of searching behaviour of Pierinae has long been suspected; antennal chemoreceptors are known to respond to glucosinolates, a major family of phytochemicals in Cruciferae (Den Otter et al., 1980). Field observations of such behaviour have been lacking until now. No females were observed to search in any other felled or wooded area, and an extensive search revealed only two more *C. flexuosa* plants in the wood; one plant bore four *P. napi* eggs.

On adopting the 'oviposition search' mode of flight, the female would investigate the ground layer of vegetation, approaching and occasionally landing upon small herbs. Females were sometimes seen deep underneath the Bracken, flying among the fronds in their search for hosts. On locating a host, a female would flutter around it, settle on a leaf and, bending the abdomen underneath, deposit an egg. On two occasions (of 32 observed ovipositions) a second egg was immediately deposited. On five other occasions the female flew up and returned to the same plant to lay a second egg. Multiple oviposition by *Pieris rapae* L is well known, but *P. napi* has rarely been seen to lay more than one egg at a host (F.S. Chew, pers. comm.). In this sub-population of dispersing individuals,

Table 2.   Average height (cm.) and leaflet number (with standard error) of *C. flexuosa* individuals growing in four categories of shading by Bracken, with the average eggload of *P. napi* on such plants (Number of eggs/Number of leaflets). Data from the marsh population are given for comparison. All data collected 28.7. 1982.

	Shading	n	Height	Leaflets	Eggload
Heath	<25%	7	9.3	5.29(1.82)	1.16
	25–50%	15	9.0	3.87(1.10)	1.12
	51–75%	14	15.0	4.86(0.90)	0.32
	>75%	26	18.1	11.69(2.61)	0.27
Marsh		35	14.1	9.20(1.31)	0.12

multiple oviposition seemed frequent, though it was never seen in the main marshy populations.

Numerous eggs were found on the 62 *C. flexuosa* individuals in the ditch. Table 2 presents these data for four groupings of plants according to the degree of overtopping by Bracken. Seven individuals had less than 25% of the sky above obscured by Bracken (estimated by eye); these plants received a very heavy load of *P. napi* eggs, with over one egg per leaflet (far more than could be supported through larval development). The majority of *C. flexuosa* were more shaded and 21 (41.9%) were almost completely obscured by Bracken. Relatively few eggs were found on heavily shaded plants, although these were the largest. Chew (1977) reports that shaded individuals of Nearctic *Cardamine* similarly escape *P. napi* oviposition. These and similar results in *Anthocharis cardamines* L. have been interpreted as consequences of females restricting their activity to areas of direct sunshine (Courtney, 1982). Note that the eggloads, of even the heavily shaded *C. flexuosa* plants in the ditch, are much heavier than those seen in the marshes where *C. flexuosa* was more plentiful. Figure 1 illustrates the combined effects of shading levels, and of host size, which also influences eggload. Similar results obtain in Nearctic *P. napi* and *Cardamine* populations (F. S. Chew, pers. comm.). Since a single *P. napi* larva would consume all the above ground biomass of a *C. flexuosa* plant, probably few hosts in the ditch escape serious grazing.

Examination of the number of eggs on the leaflets of those plants with at least one egg suggests a tendency towards clumped distributions (Table 3). The trend occurs in all three shading classes, but is significant only in the most heavily shaded class. The results contrast with data from the marsh sub-population where the distribution fortuitously agrees well with the random expectation. These results are to be expected if multiple oviposition occurs in the ditch, but not in the marsh.

Discussion

The very large eggloads, received by some *C. flexuosa* plants in the ditch, are far in excess of the number which can be supported through larval development. Courtney and Courtney (1982) described similar
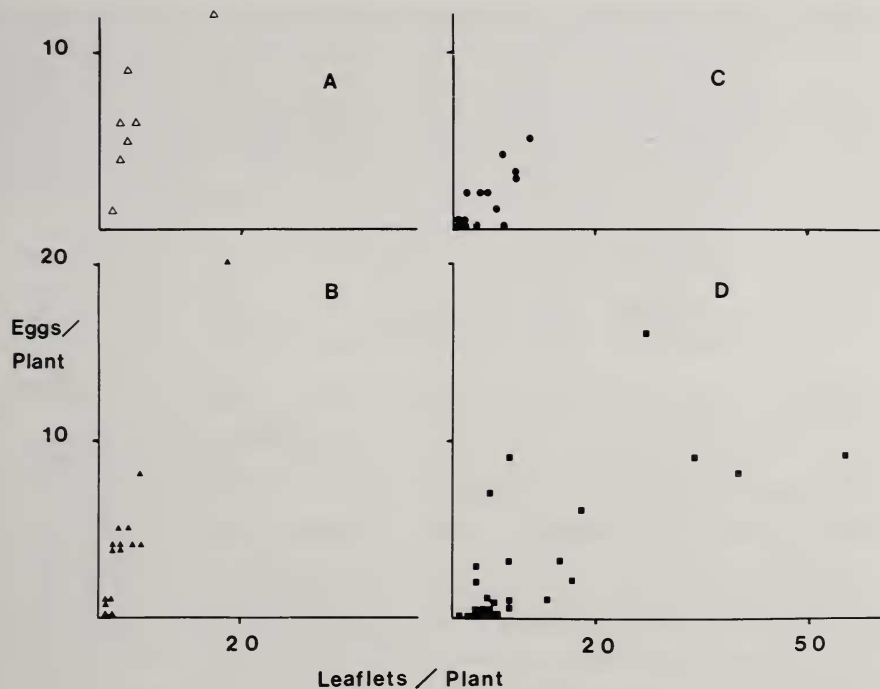
Fig. 1. The relationship between the number of leaflets on *C. flexuosa* individuals and the number of *P. napi* eggs deposited, in four categories of shading (determined by eye). The value of the correlation coefficient, r, is shown

A. (<25% of Sky obscured)   r = .810   p < 0.005
B. (25–50%)   r = .955   p < 0.001
C. (51–75%)   r = .779   p < 0.001
D. (>75%)   r = .698   p < 0.001
All data summed   r = .555   p < 0.001

inverse density dependent egg distributions in *P. napi* and *A. cardamines* and ascribed them to changes in receptivity of females. It is suggested that females accept suboptimal oviposition sites (such as those already bearing an egg or larva) when hosts are rare. The present results, which link increased eggloads to observed changes in behaviour, support the idea that females modify their behaviour in response to resource availability.

Such behaviour may have important consequences for population and community processes: Shapiro (1975) and Courtney and Courtney (1982) show how both intra- and inter-specific competition are greatly increased by clumped egg distributions. The present study suggests that such competition may be more important in peripheral habitats and in the offspring of dispersing individuals, than in main population centers. Similarly, Wiklund and Ahrberg (1978) have discussed the

Table 3.   Distributions of *P. napi* eggs over leaflets of those *C. flexuosa* plants with eggs (elimination of other plants from the analysis follows the conservative procedure of assuming that such individuals were unsuitable/unavailable for oviposition). Only three classes of shaded plant are given for the heathland site, the two lighter classes (<25% and 25−50%) being summed (mean eggloads are very similar as in Table 2). Values are given for X^2 comparisons with expected values from a random (Poisson) distribution.

| | | Eggs per leaflet | | | |
	Shading	0	1	2	3	4	5	9	X^2	d.f.	p
Heath	<50%	35	28	17	8	3	2	—	3.13	3	n.s.
	51−75%	40	10	2	1	—	1	—	1.94	2	n.s.
	>75%	231	22	9	5	2	2	1	36.90	2	<0.001
Marsh		69	17	2	—	—	—	—	0.03	2	>0.975

effect of inversely density related oviposition in a community of host-plant species which differ in their dispersion. *A. cardamines* attack was most severe on low density or highly dispersed hosts. In the present study, *P. napi* in the marsh were mainly supported by the hosts *C. pratensis* and *N. officinale*. *C. flexuosa* individuals in the marsh suffered fewer attacks than conspecifics growing alone in the ditch. It seems that the *C. flexuosa* population in the wood suffers from being in the vicinity of large marshland populations of other Cruciferae. It is a general prediction from the studies of Wiklund and Ahrberg, and of Courtney and Courtney, that peripheral species surrounding major hostplant localities may suffer disproportionately from herbivore attack.

Literature Cited

CHEW, F. S. 1975 Coevolution of Pierid butterflies and their Cruciferous food-plants. I. The relative quality of available resources. Oecologia 20: 117−127.

CHEW, F. S. 1977 II. The distribution of eggs on potential foodplants. Evolution 31: 568−579.

COURTNEY, S. P. 1982 IV. Crucifer Apparency and *Anthocharis cardamines* oviposition. Oecologia 52: 258−265.

COURTNEY, S. P. & COURTNEY S. 1982 The 'edge-effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. Ecological Entomology 7: 131−137.

DEN OTTER, C. J., BEHAN, M. & MAES, F. W. 1980 Single cell responses in female *Pieris brassicae* (Lepidoptera: Pieridae) to plant volatiles and conspecific egg odours. J. Insect Physiology 26: 465−472.

GILBERT, L. E. & SINGER, R. C. 1975 Butterfly ecology. Ann. Rev. Ecol. Syst. 6: 365−397.

PARKER, G. A. & COURTNEY, S. P. 1984 Models of Clutch Size in Insect Oviposition. Theor. Popul. Biol. 26: 27−48.

SHAPIRO, A. M. 1970 The role of sexual behavior in density related dispersal of Pierid butterflies. Am. Nat. 104: 367−373.

SHAPIRO, A. M. 1975 Ecological and behavioral aspects of coexistence in six crucifer-feeding Pierid butterflies in the central Sierra Nevada. Am. Midl. Nat. 93: 424−433.

SINGER, M. C. 1982 Quantification of host specificity by manipulation of oviposition behaviors in the butterfly *Euphydryas editha*. Oecologia 52: 224−229.

SINGER, M. C. 1984 Butterfly-hostplant relationships: host quality, adult choice and larval success. Symp. R. Ent. Soc. 11: 81−88.

TABASHNIK, B. E., WHEELOCK, H., RAINBOTT, J. D., WATT, W. B. 1981 Individual variation in oviposition preference in the butterfly *Colias eurytheme*. Oecologia 50: 225−230.

WIKLUND, C. 1981 Generalist vs. specialist behaviour in *Papili machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. Oikos 36: 163−170.

WIKLUND, C. & AHRBERG, C. 1978 Hostplants, nectar source plants and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). Oikos 31: 169−183.